# Disequilibrium and relaxation times for species responses to climate change

Craig Loehle

National Council for Air and Stream Improvement, Inc. (NCASI), 1258 Windemere Avenue, Naperville, IL, 60540, USA

ARTICLE INFO

ABSTRACT

Climate change is widely expected to pose a threat to many of Earth's plant and animal species. Based on climate models, a multitude of studies project that certain species will not be able to migrate fast enough to keep up with changing environmental conditions, presenting a greater risk of their possible extinction. However, many of these studies are based on correlative climate niche models that represent the current living conditions of species and may not consider their ability to tolerate projected changes in future climate, including the stimulative effects of rising $CO_2$ for plant growth and drought tolerance. SDMs also are not usually run with sufficiently detailed spatial data to account for refugia. These and other aspects of model-based niche studies can potentially combine to mischaracterize the risk to species due to climate change. Even a SDM that perfectly predicts future equilibrium geographic range following climate change, however, does not yield a direct estimate of extinction risk. The key question is "What is the transient response to a climate disequilibrium situation?" The concept of relaxation is introduced to evaluate time-scales for responses at the trailing edge of species' ranges. Simulation of relaxation at a forest ecotone shows the relaxation response in some cases can be hundreds of years. A classification of relaxation responses based on tolerance and dispersal ability is proposed as a second stage analysis for SDM studies.

## 1. Introduction

A number of studies postulate that anthropogenic climate change will lead to mass extinctions (Bakkenes et al., 2002; Parmesan, 2006; Parmesan and Yohe, 2003; Thomas et al., 2004; Thomas and Williamson, 2012; Urban, 2015). The most common approach used for these studies is for researchers to first examine the current geographic range and climate of a given species after which they project how future changes in climate may impact the geographic ranges. Models of factors governing species geographic ranges, called species distribution models (SDMs), climate envelope models, or niche models, are developed statistically and are used to characterize current and projected geographic ranges (Busby, 1988). Comparison between a species' current and projected climate zones (see Loarie et al., 2009) is then the basis for estimating extinction risk (Fig. 1). If climate change leads to a non-overlapping shift in a species' range (Fig. 1a) and the species cannot migrate fast enough to keep pace with the shift, it is assumed that the species will be "committed to extinction" (per Thomas et al., 2004). Another possible outcome is a range reduction. In this case (Fig. 1b), a smaller geographic range is presumed to cause a population decline, thus increasing extinction risk for that species, though not necessarily dooming it. This framework is widely used (e.g., Bakkenes et al., 2002; Breshears et al., 2008; Davis and Shaw, 2001; McKenney et al., 2007), with studies in the thousands (Booth, 2017).

A distribution model is a statistical response surface for predicting where a species will be found, either currently or in the future. The variables for predicting the distribution of a species, such as minimum winter temperature, elevation, and precipitation, are selected and a model is developed (Elith et al., 2010). However, some aspects of this approach have been questioned (e.g., Botkin et al., 2007; Dormann, 2007; Yackulic et al., 2015), it may have uncertainty resulting from method choice (Buisson et al., 2010), uncertainty in forecasts can be large (e.g., Wenger et al., 2013; Wiens et al., 2009), and results have rarely been validated (Botkin et al., 2007). Even if bioclimate models capture the realized niche, they may not make reliable predictions about the fundamental niche (Anderson, 2013; Booth, 2017; Loehle and LeBlanc, 1996) which is the climate, soils, vegetation, and other features that an organism needs for basic survival. The realized niche, in contrast, is the environment where the organism is able to persist despite biotic interactions and thus where it is actually found. The realized niche is typically much smaller, or more restrictive, than the fundamental niche and is what SDMs capture. While a few studies have evaluated both (e.g., Booth et al., 1988; Briscoe et al., 2016; Tingley et al., 2014), most have not (Booth, 2017). Thus, bioclimatic models may underestimate environmental tolerance (Araújo and Pearson, 2005; Booth, 2017; Catullo et al., 2015; Loehle, 2014; Loehle and LeBlanc, 1996; Sax et al., 2013).

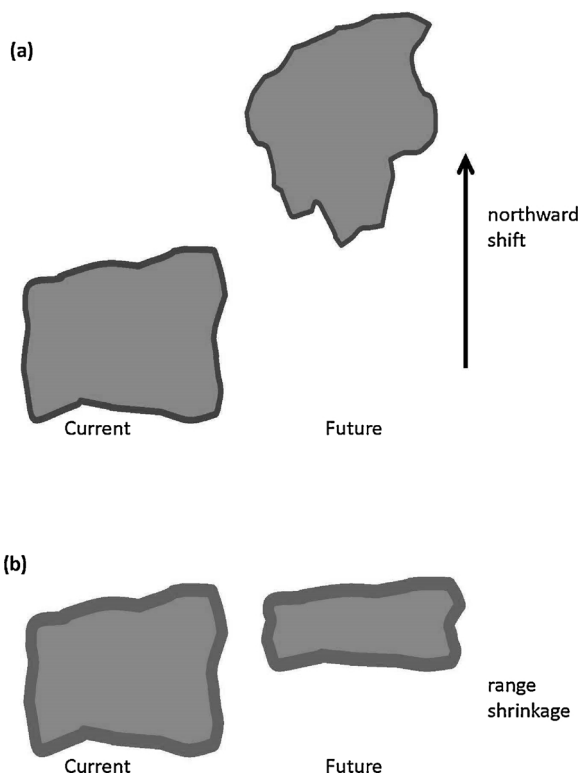A central difficulty with this approach was pointed out by Araújo

**Fig. 1.** Evaluation of current vs. projected future climate zones. (a) Poleward or upward shifts lead to non-overlapping current and future climate zones, causing extinction of species; (b) Reduction in range leads to increased risk for a species.

and Peterson (2012): extinction risk is not an explicit target of the SDM modeling approach. That is, an SDM analysis applied to future climates only predicts future equilibrium conditions and says nothing about what will happen between now and the achievement of equilibrium. If, at the trailing edge, a species can tolerate the new climate while it migrates to the new zone, then the distribution shift does not represent an increased risk of extinction. While it is known that the models are explicitly equilibrium analyses (Araújo and Peterson, 2012; Pearson and Dawson, 2003), the cautions about dynamics and tolerance of new conditions are often ignored (Pearson and Dawson, 2003) even in the most recent studies (Booth, 2017).

The problem here is not that SDMs are unrealistic (though they may be). Even a perfect future forecast does not inform us about transient responses. Another way to put this is that it is implicitly assumed that any no-overlap zone by some date (say 2100) implies reduced abundance or local extinction in that zone. This implicit response is illustrated in Fig. 3a. Growth is assumed to decline until the species cannot persist below the coldest or above the warmest temperatures (N and S respectively in the figure) implied by the current range. Thus, as soon as the temperature shifts geographically, species are assumed to find themselves in a lethal zone and quickly perish. However, this approach represents a conflation of the fundamental and realized niches. The growth response implied by Fig. 3a is not observed in nature except perhaps at the coldest and driest extremes for life where competition is minimal. Everywhere else, a species will encounter competitors long before it has a growth rate near zero (N or S in Fig. 3a). Interestingly, trailing edge retreat due to warming has so far been difficult to document, especially for plants (Intergovernmental Panel on Climate Change (IPCC), 2014; Lenoir and Svenning, 2015; Loehle, 2018). This suggests that inertia might exist due to species' tolerances of altered climate and other factors.

### 1.1. Mechanisms for disequilibrium

The dynamics of response to a change in climate should be considered when estimating extinction risk (Jackson and Sax, 2010). The time required to return from disequilibrium to a new equilibrium ("relaxation time") can be prolonged (Cole, 1985, 2009; Jackson and Sax, 2010; Loehle, 2000a; Loehle and LeBlanc, 1996) due to environmental tolerance. In addition, habitat complexity can create microclimatic refugia (Austin and van Niel, 2010; Dobrowski, 2011; Scherrer and Körner, 2010) which typically are not accounted for in niche models. For example, alpine plants found refugia during past warmer interglacials (Gentili et al., 2015), which allowed a rare endemic plant in the Alps to persist over the past 21,000 years (Patsiou et al., 2014). Lenoir et al. (2013) documented the extent to which topography creates strong spatial buffering (refugia) for plants in northern Europe. Keppel et al. (2012) summarized over 2000 studies on refugia.

Growth models have been used to predict effects of climate change on ecosystems and provide a test of the range shrinkage prediction. While these models do not have the status of experiments, they are based on mechanisms of plant growth. Growth models can incorporate effects of future increases in $CO_2$ which are likely to increase growth rates, decrease water stress, and increase the optimum temperature for photosynthesis (Tian et al., 2010; Wertin et al., 2010). These models generally predict enhanced growth over the coming century, especially if elevated $CO_2$ growth enhancements are included in the model (Loehle, 2011, 2014; Keenan et al., 2011; Cheaib et al., 2012; Kearney et al., 2010; Morin and Thuiller, 2009). Thus, rising $CO_2$ could also increase inertia for plants.

### 1.2. Historical evidence for climate tolerance

Tolerance of fluctuating climate as well as SDM reliability can be tested using historical data. The bioclimatic niche equilibrium assumption leads to predictions that 1) rapid past climate shifts should have caused extinctions, and 2) very warm past conditions should have had reduced biodiversity and caused extinctions due to the exceedance of species' thermal tolerances, especially in the tropics. Neither of these two predictions, however, appears to have much support in the paleo-literature.

A hind-cast of the location of five mammalian species' glacial refugia in North America based on current bioclimatic niche relations (Davis et al., 2014) found that the models predicted refugia far south of the actual fossil locations for all five species. This is either due to the climate envelope models or the simulated climates. Similarly, Tyrberg (2010) showed that, during the last interglacial period, multiple sites that were 2 °C warmer than present had the same avifaunal assemblages as today rather than something radically different, as implied by some models.

Toward the end of the last glacial period, rapid warming occurred multiple times, including rates much larger than has been observed over the past 100 years (Hof et al., 2011). Yet few extinctions have been identified in these periods (Hof et al., 2011), especially for plants such as trees in particular (Loehle, 2006, 2007). While some end-Pleistocene extinctions are known, they appear to have been largely precipitated by human hunting pressure (Hof et al., 2011) because their timing coincided with human arrival in each location and fossils show evidence of hunting (see citations in Loehle and Eschenbach, 2011). This evidence lends support to the hypothesis that species can be in climatic disequilibrium without extinction.

Another line of evidence for potential climate tolerance consists of the historical biogeography of endemics. In eastern North America, there are almost no endemic plants in glaciated regions due to a lack of sufficient time for endemics to have evolved since ice retreat, yet endemics can be found within a few miles of the historic ice sheet margin (Davis and Shaw, 2001; Loehle, 2006, 2007). Consequently, the hundreds of narrow endemic plants in this ice margin region likely survived

the huge climatic swings of the last glacial period or periods. This suggests considerable tolerance of climatic shifts across many species.

The gradual shift of plants to new geographic zones during past warming episodes is further evidence of their warming tolerance. Cole (1985, 2009), Cwynar and Spear (1991), and Tinner et al. (2007) showed that loss of plant species in an area (for the warm margin of shifting species) due to past increasing temperatures took one to several thousand years, whereas a somewhat faster boreal retreat occurred following cooling conditions. Jaramillo et al. (2010), in a study of the Paleocene-Eocene Thermal Maximum (PETM) 56.3 million years ago when global temperatures were elevated about 5 °C for 100,000–200,000 years, found that tropical plant speciation rates and diversity increased during this period yet extinctions were not elevated. Willis et al. (2010) found that the Eocene Climatic Optimum, 53–51 million years ago, was one of the most biodiverse times for the neotropics. During this period, the atmosphere's $CO_2$ was 1200 ppmv greater and tropical temperatures were 5–10 °C higher than today. Collectively, such findings run counter to climate envelope model assumptions that species are intolerant of warming or rapid temperature change.

### 1.3. Implications of environmental tolerance

Extensive data show that species can survive and prosper far outside their usual climate conditions, especially on the warm end. Booth (2017), Loehle (2014), and Loehle and LeBlanc (1996) showed that trees can grow in far warmer climates than might be suggested by analyses of their current natural distributions. Most Canadian trees can be found growing in botanical gardens in Australia, for example (Loehle, 2014). While botanical gardens may be (but are not necessarily) irrigated and competition is minimized, temperature is not controllable. Booth et al. (2015) found that, for many Eucalyptus species, climatic tolerance inferred from plantings outside Australia is much broader than implied by species distribution models based on their native range, an indicator of the need to consider, if possible, results from trials outside species' natural distributions (e.g., Booth, 2017). Way and Oren (2010) found that up to a 13 °C increase in growing season temperature led to increased growth for multiple temperate and boreal trees and little change for tropical trees. Pearce-Higgins et al. (2015) found that plants had the most pronounced positive responses to warming above their normal conditions, followed by invertebrates, then birds, then mammals. Amphibians showed no response and fish a negative response. It also has been shown that urban trees, due to elevated $CO_2$ in urban areas and the urban heat island effect, are growing faster than rural trees at high latitudes (Pretzsch et al., 2017) in spite of urban pollution. These authors also found increased growth for both urban and rural trees post-1960 worldwide. Trees sampled were dominant, healthy, and open-growing. These results suggest not merely tolerance for warming but growth enhancement. These positive growth study results combined with modeling results noted above contradict SDM studies claiming that rapid extinctions are likely, at least for plants.

Cold appears to be more limiting for many species than high temperatures. Szabo et al. (2009) found that, for widespread animal species of North and South America, regional biodiversity was strongly reduced by the coldest minimum temperatures with only a small reduction at the warmest minimum temperatures. Range-restricted species were less common in colder climates and enhanced by mountainous terrain. Thus, for this entire study group over the whole of the Western Hemisphere, cold appeared to be more limiting than heat. This conclusion is further supported by Davies et al. (2009), who showed that mammal species from areas with the greatest temperature increase since the last glacial maximum had the largest geographic ranges. Geographically, high northern latitude species had the largest ranges.

What do such tolerances imply for species persistence? As climate warms in the currently occupied range, the organisms in that zone may

well persist until more competitive species already within the zone or immigrating from a warmer climate out-compete them. The displacement process can take hundreds of years (Loehle, 2000a, 2014; Loehle and LeBlanc, 1996). A study of island archipelagoes led Heaney (2000) to conclude that these and other habitats are likely in a continual state of dynamic disequilibrium due to constantly changing conditions, and that such disequilibrium likely persists for prolonged periods. Brown and Lomolino (1998) further documented that many species can be found persisting within very small geographic ranges, as also noted by Loehle and Eschenbach (2011). Critically, if a species can persist for a long time in its current range, then the opportunity to migrate to a new zone may be greater than assumed by some extinction assessments. Furthermore, this means that reduced abundance at trailing edges is not an inevitable result of a climate shift.

Many attempts have been made to increase SDM realism by incorporating dispersal (e.g., Holloway and Miller, 2017). Usually, models consider no dispersal or unlimited dispersal as two bounding cases. While the inclusion of dispersal is good (and I also consider it here), it does not alleviate the reliance on assumptions that species necessarily rapidly succumb in the non-overlapping climate zone (trailing edge). The ability of species to tolerate a wider range of conditions than indicated by their current range is their environmental tolerance. The metric of concern here is how long a species can persist in an area following a climatic shift. The path followed by a population after such a change is called the transient or transient dynamics. Because of my focus on time, I here make use of the concept of relaxation time, which specifically refers to time required to "relax" back to a new equilibrium (which includes ecotone locations, geographic range, and stable patch dynamics).

Anderson (2013) and Morin and Lechowicz (2008) argued that bioclimatic niche analyses need a better focus on the biology of the fundamental niche and that mechanistic models might provide more reliable forecasts. Similarly, Yackulic et al. (2015) suggested that explicit simulation of colonization and local extinction processes is needed. The recommendation to adopt a mechanistic modeling approach seems fundamentally sound. As an example, Deutsch et al. (2008) used experimental population growth rates in response to temperature (a measure of fitness) for 38 insect species. Others have incorporated bioenergetics (Briscoe et al., 2016), bioenergetics plus behavior (Kearney et al., 2009), physiology and population biology (Fordham et al., 2013) and plant growth (Hijmans and Graham, 2006). Anderson (2013) provides a coherent set of suggestions for improving model forecasts. He shows how niche models can be built, calibrated, and tested to better represent the fundamental niche and suggests that niche model analyses be followed by a dispersal analysis (as Santini et al., 2016), although dispersal analyses often still assume that the species will perish if it cannot disperse fast enough. Finer resolution spatial data (e.g., Araújo et al., 2005; Wiens et al., 2009) would probably improve models as well by allowing for microsite refugia.

While these suggestions for improving niche models to be more mechanistic are sensible, they are labor intensive and sufficient data are often not available (Singer et al., 2016). It is therefore suggested that relaxation *per se* be more explicitly studied to provide a context for range change studies. A framework for relaxation is provided in Fig. 2. The key factors are environmental tolerance and dispersal ability. Environmental tolerance in plants is enhanced by factors such as competitive ability, physiological, phenological, and morphological plasticity, genetic heterogeneity and response (rapid evolution), long lifespan, root sprouting, seed banks, and tolerance of disturbance (e.g., fire) (Loehle, 2000b). For animals, tolerance is enhanced by migration and thermoregulatory behaviors. In the graph, trees and other plants are common in the upper left, which implies a prolonged relaxation time. Species in the upper right can both tolerate change and disperse, which implies both long relaxation times at the trailing edge and tracking change at the leading edge, giving short-term range expansion. In the lower right, species are not tolerant of change but can track their
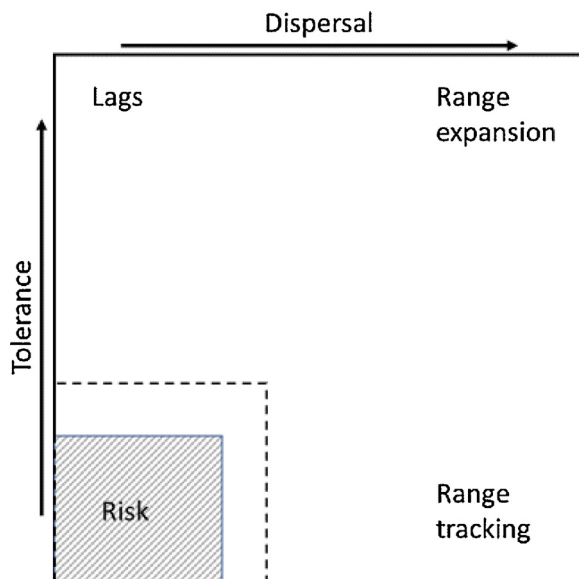
**Fig. 2.** Relaxation responses in terms of environmental tolerance and dispersal ability. In the upper left, trees (and many other plants) exemplify tolerance with slow dispersal and are likely to exhibit long relaxation times (lags) at the trailing edge of many years to centuries. At the upper right, species are likely to exhibit rapidly expanding ranges since the trailing edge does not shrink for years to centuries. At the lower right, species are likely to track climate closely (e.g., birds). Only the lower left zone will be at risk. Box lower left shows zone of risk for a moderate climate change and dashed box that for a larger climate change.

preferred climate. The lower left shaded box contains species that lack mobility and are sensitive to change. Poor dispersers include species such as earthworms and salamanders, which are unable to move long distances or cross barriers, for example. Endemics do not necessarily fall into the lower left region of Fig. 2. As noted previously, many endemics appear to have tolerated large historical climatic swings, in which case they would fall into the upper left (low risk) region, not the lower left, of Fig. 2. The size of the risk zone in the lower left of Fig. 2 will be related to the magnitude and nature of the climate change event. For a small change the shaded high-risk box might be very small.

The dispersal ability of categories of species (e.g., birds, trees) is not difficult to establish in general. Several sources of information exist to document environmental tolerance. Direct experimental studies (e.g., Pearce-Higgins et al., 2015) are particularly useful, if available. Plantings outside their native range exist for many trees (Booth, 2017; Booth et al., 2015; Loehle, 2014) and can provide valuable evidence of tolerance. A physiologically-based index of climate tolerance has been developed for trees (Liénard et al., 2016). Lifespan and disturbance resistance are often known and are useful indices of tolerance. The approach of Smith et al. (2009) could be useful for more detailed assessments. Paleo or recent studies of species shifts (cited above; also Blarquez and Aleman, 2016) can provide valuable insights. North-south geographic range also provides good evidence for niche breadth. For example, in the eastern United States many plants and animals can be found from Florida to the region around the Great Lakes, a very wide climatic zone. In very cold zones, we can predict that the response to warming should be slow due to slow plant growth (e.g., Caccianaliga and Payette, 2006). Likewise, at dry ecotones, responses should be slow except that drought could cause more rapid shifts via plant death. For certain animals, what may limit them geographically is not climate *per se* but their preferred vegetation composition or structure (e.g., trees for tree-nesting birds), in which case they would tolerate climate change and track the slower (lagged) response of the vegetation. Given this type of information, general simulations such as conducted here could provide time scales for relaxation responses for niche-based climate
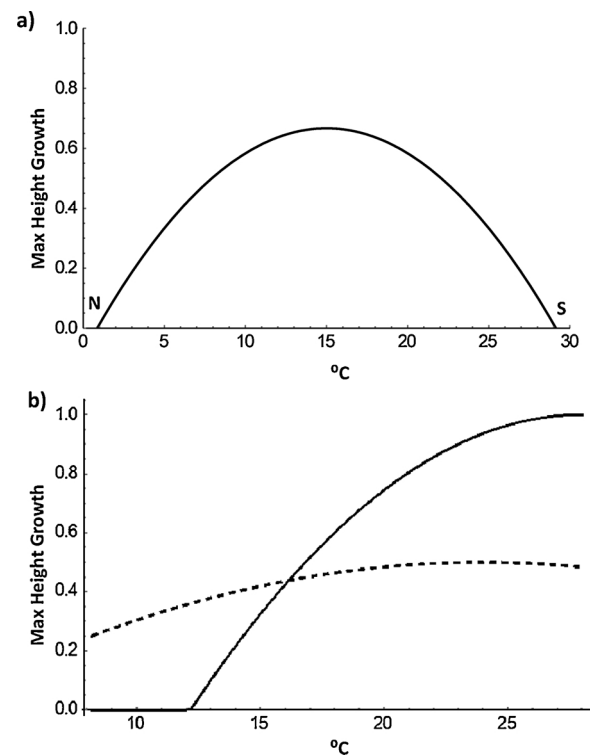


**Fig. 3.** Representative maximum annual height growth rates (m) for trees across a temperature gradient. a) Growth response implied by SDMs, with N and S representing northern and southern range margins. b) More realistic growth responses implied by wider climatic tolerance and observed growth enhancements outside the current range (solid line is northern type; dashed line is southern type). Where the lines cross, we expect an ecotone.

change studies based on general species responses. At this stage what can be said is that four outcomes are likely: prolonged relaxation (no reduction in abundance); prolonged relaxation plus dispersal (range expansion); rapid dispersal (climate tracking); and poor dispersal plus intolerance. Only the last case represents species at risk.

At this point it is useful to illustrate how relaxation times can be estimated from models. These relaxation times can inform the analysis in Fig. 2 without needing to be exact. For example, if a simple model shows a relaxation time (for local extinction) of hundreds of years, then concern about that species over the next few decades can probably be put aside.

## 2. Methods

I modeled responses of two tree species to temperature along an elevational ecotone using *Mathematica*, with competition based on height growth. Maximum annual height growth was based on temperature (Fig. 3b) with the prediction that abundance would differ across the ecotone defined by the intersection of their growth curves. Note that, across the entire range of temperature, both species grow better with warmer conditions. The tradeoff of growth rate vs. cold tolerance was based on Loehle (1998) and Pearce-Higgins et al. (2015) who showed that plants generally respond positively to warming. The height growth response to temperature is given by Eqs. (1) and (2).

$$G = g_{max} - a\,(t - b)^2 \tag{1}$$

$$t = 8 + i/5 \tag{2}$$

where $i$ is the elevational grid square or cell, $t$ is temperature (°C), $G$ is height growth per year, $g_{max}$ is maximum height growth per year (m), and $a$, $b$ are shape parameters. Values for parameters were chosen to represent typical tree responses (Loehle, 1998; Loehle and LeBlanc,

1996), with $g_{max}$, $a$, and $b$ {0.5, 0.001, 24} for the upper elevation species and {1.0, 0.004, 28} for the lower elevational species, respectively. This is a deliberately simplistic model, for illustrative purposes only.

The elevational ecotone was modeled on a one-year time-step using a $100 \times 100$ cell grid of $10 \times 10$ m cells. Each cell was assumed to support one adult tree (age $\geq 15$). Tree death occurred randomly on cells with a probability of 0.02/yr to produce a mean lifespan of about 50 years. Trees colonized vacant cells (no adult trees) from the four cardinal locations with probability 0.2/year/grid until year 15 when the tallest tree in the cell dominated and the others died. Colonization wrapped on a torus across the elevations (horizontally). The first tree to colonize did not necessarily occupy the site at year 15 if the other species grew better at that temperature and overtook it. The elevational lapse rate was $20^0 C/1000$ m. This high lapse rate was chosen to allow an ecotone to develop in a reasonable sized grid. The site was initialized by assigning each cell randomly to one of the two species with an initial age of 100 years and was then run to equilibrium to verify the ecotone location, itself a relaxation response. Once equilibrium was established, I conducted a warming experiment by adding 2 °C to the elevational temperature gradient (Eq. (2)) and evaluated the rate of ecotone shift.

A second model was chosen to represent conditions away from an ecotone. A metapopulation approach (see Talluto et al., 2017) was used. Each of 1000 cells was initially occupied. Colonization and dispersal were modeled, with universal dispersal (not neighborhood) within the simulated area, which was not large. Parameters were changed at time 0 to colonization = 0.02 and extinction = 0.022 per cell per year. Again, this is a deliberately simplistic model simply for illustration.

## 3. Results

Due to the long lifespan of trees, it required almost 500 years for equilibrium to be reached from the initial random state (Fig. 4a). At equilibrium, average age of adult trees (above the age 15 cutoff) was approximately 50 years, representing a young forest with high turnover. For long-lived trees, the transient response can be much longer (Loehle, 2000a). Adding disturbance or using other parameters would alter results. After the step warming of 2 °C, the ecotone shifted smoothly over a 500 yr period (Fig. 4b). Ecotone locations and shapes after 500 years were visually similar to the 500 year curve. There was no sudden reduction in abundance or dieback at the trailing edge. Multiple repetitions of the simulation yielded results visually the same as Fig. 4. Because the results are for purposes of illustration, I did not calculate or present a measure of variance in time or in ecotone shape. The point is that transition times are prolonged, not sudden.

The metapopulation results are shown in Fig. 5. Relaxation to the new stable state is clearly shown, with a new equilibrium being reached in about 60 years. This result is specific to the parameters chosen.

## 4. Discussion

The ecotone simulations (Figs. 4,5) illustrate two key facts about geographic ranges. First, a range boundary or ecotone can be governed by competition even when both species respond positively to warming. Even if the species grows better outside its current range in the absence of competition, it will have a smaller realized niche due to the existence of competitors. The existence of evolutionary growth tradeoffs (Loehle, 1998) makes this likely in general. This is the SDM paradox: bioclimatic niche models can make correct range predictions, both in the present and at future equilibrium, without being correct about risk during transients. Second, the relaxation response can be prolonged. In the case simulated, it took 500 years in spite of a clear competitive advantage for the warm-habitat species either to relax from random to an ecotone or for the ecotone to respond after warming. For longer-lived species, it would take even longer (Loehle, 2000a). In the
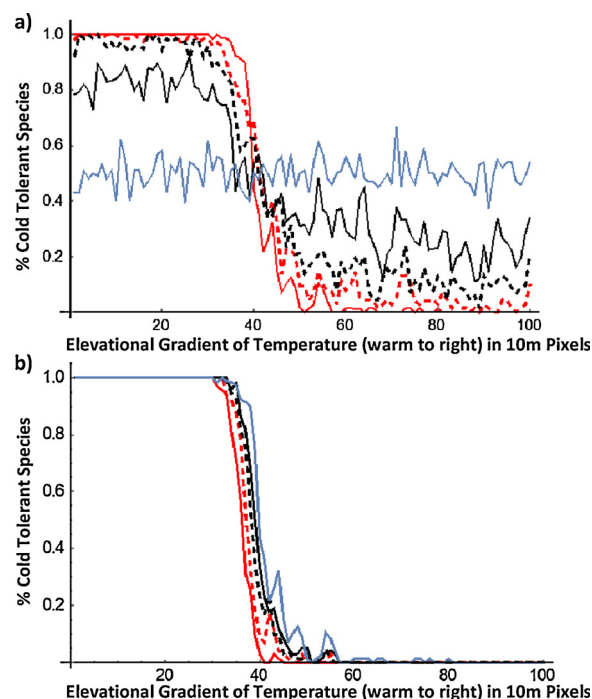


**Fig. 4.** Ecotones resulting from competition. a) Equilibrium ecotone (% northern or cold type) vs. competition tradeoff point from Fig. 2. Blue, initial. Black, 100 yr. Dashed, 200 yr. Red dashed, 300 yr. Red, 500 yr. b) Ecotone shift with time in response to a 2°C warm increment. Same color scheme (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
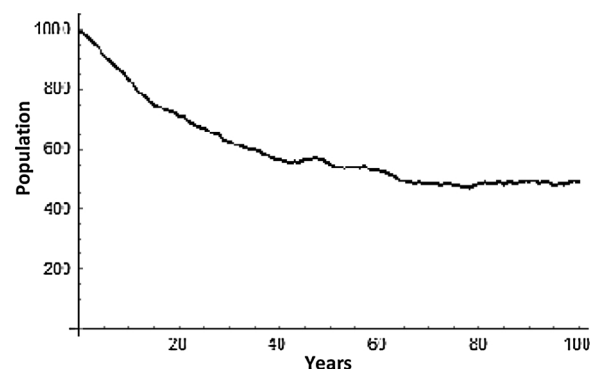


**Fig. 5.** Metapopulation example relaxation following increased mortality rates.

metapopulation case, relaxation took 60 years.

It is critical to explicitly state assumptions in climate change impact studies, and assumptions that species must migrate to their new ideal range or perish may not be valid. When studying transient response to change it is important to consider relaxation times at the trailing edge, not just migration rates at the leading edge. This study provides a framework for such analyses. It is therefore suggested that, following an equilibrium (SDM or other) analysis, a relaxation analysis be applied to bridge the causal gap to infer risk to species. Otherwise, projections of risk (e.g., Urban, 2015) may suffer from an unrecognized bias.

## Funding

## Acknowledgement

## References

Anderson, R.P., 2013. A framework for using niche models to estimate impacts of climate change on species distributions. Ann. N. Y. Acad. Sci. 1297, 8–28. http://dx.doi.org/10.1111/nyas.12264.

Araújo, M.B., Pearson, R.G., 2005. Equilibrium of species' distributions with climate. Ecography 28, 693–695. http://dx.doi.org/10.1111/j.2005.0906-7590.04253.x.

Araújo, M.B., Peterson, A.T., 2012. Uses and misuses of bioclimatic envelope modeling. Ecology 93, 1527–1539.

Araújo, M.B., Thuiller, W., Williams, P.H., Reginster, I., 2005. Downscaling European species atlas distributions to a finer resolution: implications for conservation planning. Glob. Ecol. Biogeogr. 14, 17–30. http://dx.doi.org/10.1111/j.1466-822X.2004.00128.x.

Austin, M.P., van Niel, K.P., 2010. Improving species distribution models for climate change. J. Biogeogr. 38, 1–8. http://dx.doi.org/10.1111/j.1365-2699.2010.02416.x.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., Latour, J.B., 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Glob. Change Biol. 8, 390–407. http://dx.doi.org/10.1046/j.1354-1013.2001.00467.x.

Blarquez, O., Aleman, J.C., 2016. Tree biomass reconstruction shows no lag in postglacial afforestation of eastern Canada. Can. J. For. Res. 46, 485–498. http://dx.doi.org/10.1139/cjfr-2015-0201.

Booth, T.H., 2017. Assessing species climatic requirements beyond the realized niche: some lessons mainly from tree species distribution modelling. Clim. Change 2017, 1–13. http://dx.doi.org/10.1007/s10584-017-2107-9.

Booth, T.H., Nix, H.A., Hutchinson, M.F., Jovanic, T., 1988. Niche analysis and tree species introduction. For. Ecol. Manage. 23, 47–59. http://dx.doi.org/10.1016/0378-1127(88)90013-8.

Booth, T.H., Broadhurst, L.M., Pinkard, E., Prober, S.M., Dillon, S.K., Bush, D., Pinyopusarerk, K., Doran, J.C., Ivkovich, M., Young, A.G., 2015. Native forests and climate change: lessons from eucalypts. For. Ecol. Manage. 347, 18–29. http://dx.doi.org/10.1016/j.foreco.2015.03.002.

Botkin, D.B., Saxe, H., Araújo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson, P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert, D.W., Loehle, C., Margules, C., New, M., Sobel, M.J., Stockwell, D.R.B., 2007. Forecasting effects of global warming on biodiversity. Bioscience 57, 227–236. http://dx.doi.org/10.1641/B570306.

Breshears, D.D., Huxman, T.E., Adams, H.D., Zou, C.B., Davison, J.E., 2008. Vegetation synchronously leans upslope as climate warms. Proc. Natl. Acad. Sci. U. S. A. 105, 11591–11592. http://dx.doi.org/10.1073/pnas.0806579105.

Briscoe, N.J., Kearney, M.R., Taylor, C.A., Wintle, B.A., 2016. Unpacking the mechanisms captured by a correlative species distribution model to improve predictions of climate refugia. Glob. Change Biol. 22, 2425–2439. http://dx.doi.org/10.1111/gcb.13280.

Brown, J., Lomolino, M., 1998. Biogeography, 2nd ed. Sinauer, Sunderland MA.

Buisson, L., Thuiller, W., Casajus, N., Lek, S., Grenouillet, G., 2010. Uncertainty in ensemble forecasting of species distribution. Glob. Change Biol. 16, 1145–1157. http://dx.doi.org/10.1111/j.1365-2486.2009.02000.x.

Busby, J.R., 1988. Potential impacts of climate change on Australia's flora and fauna. In: Pearman, G.I. (Ed.), Greenhouse: Planning for Climate Change. Commonwealth Scientific and Industrial Research Organisation (CSIRO), Melbourne, pp. 387–398.

Caccianiga, M., Payette, S., 2006. Recent advance of white spruce (*Picea glauca*) in the coastal tundra of the eastern shore of Hudson Bay (Québec, Canada). J. Biogeogr. 33, 2120–2135. http://dx.doi.org/10.1111/j.1365-2699.2006.01563.x.

Catullo, R.A., Ferrier, S., Hoffmann, A.A., 2015. Extending spatial modelling of climate change responses beyond the realized niche: estimating and accommodating, physiological limits and adaptive evolution. Glob. Ecol. Biogeogr. 24, 1192–1202.

Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E.S., Legay, M., Pagé, C., Thuiller, W., Viovy, N., Leadley, P., 2012. Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. Ecol. Lett. 15, 533–544. http://dx.doi.org/10.1111/j.1461-0248.2012.01764.x.

Cole, K., 1985. Past rates of change, species richness and a model of vegetational inertia in the Grand Canyon. Ariz. Am. Nat. 125, 289–303. http://dx.doi.org/10.1086/284341.

Cole, K.L., 2009. Vegetation response to early Holocene warming as an analog for current and future changes. Conserv. Biol. 24, 29–37. http://dx.doi.org/10.1111/j.1523-1739.2009.01406.x.

Cwynar, L.C., Spear, R.W., 1991. Reversion of forest to tundra in the central Yukon. Ecology 72, 202–212. http://dx.doi.org/10.2307/1938915.

Davies, T.J., Purvis, A., Gittleman, J.L., 2009. Quaternary climate change and the geographic range of mammals. Am. Nat. 174, 297–307. http://dx.doi.org/10.1086/603614.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. Science 292, 673–679. http://dx.doi.org/10.1126/science.292.5517.673.

Davis, E.B., McGuire, J.L., Orcutt, J.D., 2014. Ecological niche models of mammalian glacial refugia show consistent bias. Ecography 37, 1133–1138. http://dx.doi.org/10.1111/ecog.01294.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. 105, 6668–6672. http://dx.doi.org/10.1073/pnas.0709472105.

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Change Biol. 17, 1022–1035. http://dx.doi.org/10.1111/j.1365-2486.2010.02263.x.

Dormann, C.F., 2007. Promising the future? Global change projections of species distributions. Basic Appl. Ecol. 8, 387–397. http://dx.doi.org/10.1016/j.baae.2006.11.001.

Elith, J., Kearney, M., Phillips, S., 2010. The art of modelling range-shifting species. Methods Ecol. Evol. 1, 330–342. http://dx.doi.org/10.1111/j.2041-210X.2010.00036.x.

Fordham, D.A., Mellin, C., Russell, B.D., Akçakaya, R.H., Bradshaw, C.J.A., Aiello-Lammens, M.E., Caley, J.M., Connell, S.D., Mayfield, S., Shepherd, S.A., Brook, B.W., 2013. Population dynamics can be more important than physiological limits for determining range shifts under climate change. Glob. Change Biol. 19, 3224–3237. http://dx.doi.org/10.1111/gcb.12289.

Gentili, R., Baroni, C., Caccianiga, M., Armiraglio, S., Ghiani, A., Citterio, S., 2015. Potential warm-stage microrefugia for alpine plants: feedback between geomorphological and biological processes. Ecol. Complex. 21, 87–99. http://dx.doi.org/10.1016/j.ecocom.2014.11.006.

Heaney, L.R., 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Glob. Ecol. Biogeogr. 9, 59–74. http://dx.doi.org/10.1046/j.1365-2699.2000.00163.x.

Hijmans, R.J., Graham, C.H., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Glob. Change Biol. 12, 2272–2281. http://dx.doi.org/10.1111/j.1365-2486.2006.01256.x.

Hof, C., Levinsky, I., Araújo, M.B., Rahbek, C., 2011. Rethinking species' ability to cope with rapid climate change. Glob. Change Biol. 17, 2987–2990. http://dx.doi.org/10.1111/j.1365-2486.2011.02418.x.

Holloway, P., Miller, J.A., 2017. A quantitative synthesis of the movement concepts used within species distribution modelling. Ecol. Modell. 356, 91–103. http://dx.doi.org/10.1016/j.ecolmodel.2017.04.005.

Intergovernmental Panel on Climate Change (IPCC), 2014. Fifth Assessment Report (AR5). Available online:. Working Group II (WGII). http://www.ipcc.ch/.

Jackson, S.T., Sax, D.F., 2010. Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. Trends Ecol. Evol. 25, 153–160. http://dx.doi.org/10.1016/j.tree.2009.10.001.

Jaramillo, C., Ochoa, D., Contreras, L., Pagani, M., Carvajal-Ortiz, H., Pratt, L.M., Krishnan, S., Cardona, A., Romero, M., Quiroz, L., Rodriguez, G., Rueda, M.J., de la Parra, F., Morón, S., Green, W., Gayona, G., Montes, C., Quintero, O., Ramirez, R., Mora, G., Schouten, S., Bermudez, H., Navarrete, R., Parra, G., Alvarán, M., Osorno, J., Crowley, J.L., Valencia, V., Vervoort, J., 2010. Effects of rapid global warming at the paleocene-eocene boundary on neotropical vegetation. Science 330, 957–961. http://dx.doi.org/10.1126/science.1193833.

Kearney, M., Shine, R., Porter, W.P., 2009. The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proc. Natl. Acad. Sci. 106, 3835–3840. http://dx.doi.org/10.1073/pnas.0808913106.

Kearney, M.R., Wintle, B.A., Porter, W.P., 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conserv. Lett. 3, 203–213. http://dx.doi.org/10.1111/j.1755-263X.2010.00097.x.

Keenan, T., Maria Serra, J., Lloret, F., Ninyerola, M., Sabate, S., 2011. Predicting the future of forests in the Mediterranean under climate change, with niche- and process-based models: $CO_2$ matters!. Glob. Change Biol. 17, 565–579. http://dx.doi.org/10.1111/j.1365-2486.2010.02254.x.

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Schut, A.G.T., Hopper, S.D., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Glob. Ecol. Biogeogr. 21, 393–404. http://dx.doi.org/10.1111/j.1466-8238.2011.00686.x.

Lenoir, J., Svenning, J.-C., 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. Ecography 38, 15–28. http://dx.doi.org/10.1111/ecog.00967.

Lenoir, J., Graae, B.J., Aarrestad, P.A., Alsos, I.G., Armbruster, W.S., Austrheim, G., Bergendorff, C., Birks, H.J.B., Bråthen, K.A., Brunet, J., Brunn, H.H., Dahlberg, C.J., Decocq, G., Diekmann, M., Dynesius, M., Ejrnæs, R., Grytnes, J.-A., Hylander, K., Klanderud, K., Luoto, M., Milbau, A., Moora, M., Nygaard, B., Odland, A., Ravolainen, V.T., Reinhardt, S., Sandvik, S.M., Schei, F.H., Speed, J.D.M., Tveraabak, L.U., Vandvik, V., Velle, L.G., Virtanen, R., Zobel, M., Svenning, J.-C., 2013. Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across northern Europe. Glob. Change Biol. 19, 1470–1481. http://dx.doi.org/10.1111/gcb.12129.

Liénard, J., Harrison, J., Strigul, N., 2016. US forest response to projected climate-related stress: a tolerance perspective. Glob. Change Biol. 22, 2875–2886. http://dx.doi.org/10.1111/gcb.13291.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B., Ackerly, D.D., 2009. The velocity of climate change. Nature 462. http://dx.doi.org/10.1038/nature08649.

Loehle, C., 1998. Height growth rate tradeoffs determine northern and southern range limits for trees. J. Biogeogr. 25, 735–742. http://dx.doi.org/10.1046/j.1365-2699.1998.2540735.x.

Loehle, C., 2000a. Forest ecotone response to climate change: sensitivity to temperature response functional forms. Can. J. For. Res. 30, 1632–1645.

Loehle, C., 2000b. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. Am. Nat. 156, 14–33. http://dx.doi.org/10.1086/303369.

Loehle, C., 2006. Endemic plant distribution in eastern North America: implications for conservation. J. For. 104, 415–418.

Loehle, C., 2007. Predicting pleistocene climate from vegetation in North America. Clim. Past 3, 109–118.

Loehle, C., 2011. Criteria for assessing climate change impacts on ecosystems. Ecol. Evol. 1, 63–72. http://dx.doi.org/10.1002/ece3.7.

Loehle, C., 2014. Climate change is unlikely to cause a biodiversity crisis: evidence from northern latitude tree responses to warming. Energy Environ. 25, 147–153.

Loehle, C., (submitted). Geographic range changes due to climate change: a review of trends for northern hemisphere terrestrial species. *Ecography*.

Loehle, C., Eschenbach, W., 2011. Historical bird and terrestrial mammal extinction rates and causes. Divers. Distrib. 18, 84–91. http://dx.doi.org/10.1111/j.1472-4642.2011.00856.x.

Loehle, C., LeBlanc, D.C., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecol. Modell. 90, 1–31. http://dx.doi.org/10.1016/0304-3800(96)83709-4.

McKenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K., Hutchinson, M.F., 2007. Potential impacts of climate change on the distribution of North American trees. Bioscience 57, 939–948. http://dx.doi.org/10.1641/B571106.

Morin, X., Lechowicz, M.J., 2008. Contemporary perspectives on the niche that can improve models of species range shifts under climate change. Biol. Lett. 4, 573–576. http://dx.doi.org/10.1098/rsbl.2008.0181.

Morin, X., Thuiller, W., 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. Ecology 90, 1301–1313. http://dx.doi.org/10.1890/08-0134.1.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Ann. Rev. Ecol. Evol. Syst. 37, 637–669. http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110100.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42. http://dx.doi.org/10.1038/nature01286.

Patsiou, T.S., Conti, E., Zimmermann, N.E., Theodoridis, S., Randin, C.F., 2014. Topo-climatic microrefugia explain the persistence of a rare endemic plant in the Alps during the last 21 millennia. Glob. Change Biol. 20, 2286–2300. http://dx.doi.org/10.1111/gcb.12515.

Pearce-Higgins, J.W., Ockendon, N., Baker, D.J., Carr, J., White, E.C., Almond, R.E.A., Amano, T., Bertram, E., Bradbury, R.B., Bradley, C., Burchart, S.H.M., Doswald, N., Foden, W., Gill, D.J.C., Green, R.E., Sutherland, W.J., Tanner, E.V.J., 2015. Geographical variation in species' population responses to changes in temperature and precipitation. Proc. Roy. Soc. B 282, 20151561. http://dx.doi.org/10.1098/rspb.2015.1561.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeol. 12, 361–371.

Pretzsch, H., Biber, P., Uhl, E., Dahlhausen, J., Schütze, G., Perkins, D., Rötzer, T., Caldentey, J., Koike, T., van Con, T., Chavanne, A., du Toit, B., Foster, K., Lefer, B., 2017. Climate change accelerates growth of urban trees in metropolises worldwide. Sci. Rep. 7, 15403. http://dx.doi.org/10.1038/s41598-017-14831-w.

Santini, L., Cornulier, T., Bullock, J.M., Palmer, S.C.F., White, S.M., Hodgson, J.A., Bocedi, G., Travis, J.M.J., 2016. A trait-based approach for predicting species responses to environmental change from sparse data: how well might terrestrial mammals track climate change? Glob. Change Biol. 22, 2415–2424. http://dx.doi.org/10.1111/gcb.13271.

Sax, D.F., Early, R., Bellemare, J., 2013. Niche syndromes, species extinction risks, and management under climate change. Trends Ecol. Evol. 28, 517–523.

Scherrer, D., Körner, C., 2010. Infra-red thermometry of alpine landscapes challenges climatic warming projections. Glob. Change Biol. 16, 2602–2613. http://dx.doi.org/10.1111/j.1365-2486.2009.02122.x.

Singer, A., Johst, K., Banitz, T., Fowler, M.S., Groeneveld, J., Gutiérrez, A.G., Hartig, F., Krug, R.M., Liess, M., Matlack, G., Meyer, K.M., Pe'er, G., Radchuk, V., Voinopol-Sassu, A.-J., Travis, J.M.J., 2016. Community dynamics under environmental change: how can next generation mechanistic models improve projections of species distributions? Ecol. Modell. 326, 63–74. http://dx.doi.org/10.1016/j.ecolmodel.2015.11.007.

Smith, M.D., Knapp, A.K., Collins, S.L., 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. Ecology 90, 3279–3289.

Szabo, N.D., Algar, A.C., Kerr, J.T., 2009. Reconciling topographic and climatic effects on widespread and range-restricted species richness. Glob. Ecol. Biogeogr. 18, 735–744. http://dx.doi.org/10.1111/j.1466-8238.2009.00479.x.

Talluto, M.V., Boulangeat, I., Vissault, S., Thuiller, W., Gravel, D., 2017. Extinction debt and colonization credit delay range shifts of eastern North American trees. Nat. Ecol. Evol. 1, 0182. http://dx.doi.org/10.1038/s41559-017-0182.

Thomas, C.D., Williamson, M., 2012. Extinction and climate change. Nature 482, E4–E5. http://dx.doi.org/10.1038/nature10858.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Sinqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148. http://dx.doi.org/10.1038/nature02121.

Tian, H., Chen, G., Liu, M., Zhang, C., Sun, G., Lu, C., Xu, X., Ren, W., Pan, S., Chappelka, A., 2010. Model estimates of net primary productivity, evapotranspiration, and water use efficiency in the terrestrial ecosystems of the southern United States during 1895-2007. For. Ecol. Manag. 259, 1311–1327. http://dx.doi.org/10.1016/j.foreco.2009.10.009.

Tingley, R., Vallinoto, M., Sequeira, F., Kearney, M.R., 2014. Realized niche shift during a global biological invasion. Proc. Natl. Acad. Sci. 111, 10233–10238. http://dx.doi.org/10.1073/pnas.1405766111.

Tinner, W., Bigler, C., Gedye, S., Gregory-Eaves, I., Jones, R.T., Kaltenrieder, P., Krähenbühl, U., Hu, F.S., 2007. A 700-year paleoecological record of boreal ecosystem response to climatic variation from Alaska. Ecology 89, 729–743. http://dx.doi.org/10.1890/06-1420.1.

Tyrberg, T., 2010. Avifaunal responses to warm climate: the message from last interglacial faunas. Rec. Aust. Mus. 62, 193–205.

Urban, M.C.M.C., 2015. Accelerating extinction risk from climate change. Science 348, 571–573. http://dx.doi.org/10.1126/science.aaa4984.

Way, D.A., Oren, R., 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. Tree Physiol. 30, 669–688. http://dx.doi.org/10.1093/treephys/tpq015.

Wenger, S.J., Som, N.A., Dauwalter, D.C., Isaak, D.J., Neville, H.M., Luce, C.H., Dunham, J.B., Young, M.K., Fausch, K.D., Rieman, B.E., 2013. Probabilistic accounting of uncertainty in forecasts of species distributions under climate change. Glob. Change Biol. 19, 3343–3354. http://dx.doi.org/10.1111/gcb.12294.

Wertin, T.M., McGuire, M.A., Teskey, R.O., 2010. The influence of elevated temperature, elevated atmospheric CO2 concentration and water stress on net photosynthesis of loblolly pine (Pinus taeda L.) at northern, central and southern sites in its native range. Glob. Change Biol. 16, 2089–2103. http://dx.doi.org/10.1111/j.1365-2486.2009.02053.x.

Wiens, J.A., Stralberg, D., Jongsomjit, D., Howell, C.A., Snyder, M.A., 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. Proc. Natl. Acad. Sci. 106, 19729–19736. http://dx.doi.org/10.1073/pnas.0901639106.

Willis, K.J., Bennett, K.D., Bhagwat, S.A., Birks, H.J.B., 2010. 4 °C and beyond: what did this mean for biodiversity in the past? Syst. Biodivers. 8, 3–9. http://dx.doi.org/10.1080/14772000903495833.

Yackulic, C.B., Nichols, J.D., Reid, J., Der, R., 2015. To predict the niche, model colonization and extinction. Ecology 96, 16–23. http://dx.doi.org/10.1890/14-1361.1.